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Rana (Pelophylax) ridibunda Pallas, 1771, *Rana (Pelophylax) perezi* Seoane, 1885 and their associated klepton (Amphibia, Anura) : morphological diagnoses and description of a new taxon

by Pierre-André CROCHET, Alain DUBOIS, Annemarie OHLER & Heinz TUNNER

Abstract. — Specimens of green frogs from Southern France belonging to the species *Rana (Pelophylax) perezi* Seoane, 1885 and to its associated klepton were identified by enzyme electrophoresis. These specimens, as well as specimens of *Rana (Pelophylax) ridibunda* Pallas, 1771 from Poland, were submitted to a morphometrical analysis, which allowed to find diagnostic measurements and ratios for the three taxa. These allow to confirm the identification of the lectotypes of *Rana fortis* Boulenger, 1884 (currently considered a subjective synonym of *Rana ridibunda*, but which might prove to be a distinct taxon) and of *Rana esculenta perezi*. Both these lectotypes are redescribed. A Latin scientific name and a description are also provided for the klepton associated in Southern France and North-Eastern Spain with *Rana perezi*, and which was until now known as "Graf's frog" or "*Rana* kl. RP".

Keywords. — Green frogs, *Rana ridibunda, Rana perezi*, klepton, Graf's frog, electrophoresis, morphometry, diagnostic measurements and ratios.

Rana (Pelophylax) ridibunda Pallas, 1771, *Rana (Pelophylax) perezi* Seoane, 1885 et leur klepton associé (Amphibia, Anura) : diagnoses morphologiques et description d'un nouveau taxon

Résumé. — Des spécimens de grenouilles vertes du sud de la France appartenant à l'espèce *Rana (Pelophylax) perezi* Seoane, 1885 et à son klepton associé ont été identifiés par électrophorèse de protéines. Ces spécimens, ainsi que des spécimens de *Rana (Pelophylax) ridibunda* Pallas, 1771 de Pologne, ont été soumis à une analyse morphométrique, qui a permis de trouver des mesures et des rapports de mesures diagnostiques pour les trois taxons. Ces critères permettent de confirmer l'identification des lectotypes de *Rana fortis* Boulenger, 1884 (nom actuellement considéré comme un synonyme subjectif de *Rana ridibunda*, mais qui pourrait s'avérer représenter un taxon distinct) et de *Rana esculenta perezi*. Ces deux lectotypes sont redécrits. Un nom scientifique latin et une description sont aussi proposés pour le klepton associé dans le sud de la France et le nord-est de l'Espagne avec *Rana perezi*, et qui était jusqu'à présent connu sous les noms de « grenouille de Graf » ou de « *Rana* kl. RP ».

Mots-clés. — Grenouilles vertes, *Rana ridibunda*, *Rana perezi*, klepton, grenouille de Graf, électrophorèse, morphométrie, mesures et rapports diagnostiques.

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INTRODUCTION

The systematics of European green frogs had a bursting development in the last decades (BERGER, 1973; HOTZ, 1974; DUBOIS, 1977; GÜNTHER, 1979; GRAF & POLLS PELAZ, 1989; GÜNTHER, 1990; DUBOIS & OHLER, 1995*a-b*). The high level of variation occurring among these frogs has been observed for a long time, a fact which is reflected in the very heavy synonymies in this group (DUBOIS & OHLER, 1995*a-b*). Nevertheless, the biological status of the described taxa started being understood only in the beginning of the seventies (TUNNER, 1973). This group contains not only biological species, but also special hybridogenetic taxons, known as kleptons (DUBOIS & GÜNTHER, 1982; DUBOIS, 1991).

A distinct green frog taxon from the Iberian Peninsula and Southern France was described as *Rana esculenta perezi* by SEOANE in 1885. It was long considered to be a subspecies of *Rana ridibunda* (MERTENS & WERMUTH, 1960). An electrophoretic study by GRAF *et al.* (1977) showed not only that it is a distinct species (HOTZ, 1974), but also that it is associated in Southern France with a particular hybridogenetic taxon, which has been named "Graf's frog" (DUBOIS, 1982) or "*Rana* kl. RP" (GRAF & POLLS PELAZ, 1989). The genotype of this klepton is composed of one genome from *Rana perezi* and one genome from *Rana ridibunda* (GRAF & POLLS PELAZ, 1989). The association between *Rana perezi* and Graf's frog was later shown to occur also is the north-eastern part of Spain (UZZELL & TUNNER, 1983; ARANO *et al.*, 1995).

The electrophoretic discrimination between *Rana perezi* and its associated klepton raises no particular problem. However, the morphological determination of these two taxa is not currently possible. For field studies and for studies of fixed collection specimens, it would appear very useful to know morphological characters that would allow to discriminate the two forms. If such characters can be found, they will also allow to check the status of old type-specimens and to solve nomenclatural problems (DUBOIS & OHLER, 1995*a-b*).

In order to explore this question, we carried out a morphometrical study of specimens of green frogs from several localities in Southern France belonging to the species *Rana perezi* and to its associated klepton. These specimens had been ascribed to their respective taxa on the basis of enzyme electrophoresis. The morphometrical analysis allowed to discover several discriminant morphometrical characters for the two taxa. These characters will allow to ascribe old specimens, including types of ancient nominal taxa, to either of the two biological taxa.

For sake of comparison, we took measurements on a series of specimens of *Rana ridibunda* from Poland collected and determined by Leszek BERGER, and we provide information on diagnostic morphometrical characters between this species and the two other green frogs mentioned above.

Rana esculenta perezi was described upon a series of syntypes and the name *perezi* is currently used by specialists of European green frogs for the Iberian and Southern French biological species, *i.e.* the non-hybrid taxon. We had the opportunity to study two of the syntypes of this nominal taxon, including the recently designated lectotype (DUBOIS & OHLER, 1995*a*).

For the associated klepton, we first assumed (DUBOIS & OHLER, 1995*a*) that there was a name available: *Rana maritima* Risso, 1827. This name was based on green frogs from Southern France ("Alpes-Maritimes", as defined at the beginning of the nineteenth century), a region where both *Rana perezi* and Graf's klepton were believed to occur according to the maps published by GRAF & POLLS PELAZ (1989) and CASTANET & GUYÉTANT (1989). Since then, we carried

out field investigations in order to clarify the biological status of frogs in this part of France: these researches showed the occurrence of Italian taxa in this area (DUBOIS & OHLER, 1995*b*; CROCHET *et al.*, in preparation). As a consequence, the name *Rana maritima* Risso, 1827 is available for Italian green frogs, but not for Graf's frog. Resolution of this nomenclatural problem leaves no more name available for Graf's frog, so that we are led to name it in this paper.

A description of the lectotype of *Rana fortis* Boulenger, 1884 (DUBOIS & OHLER, 1995*a*) is also included in this paper. The taxon *Rana ridibunda* as currently understood is probably heterogeneous (GÜNTHER, 1982). Mating calls of *Rana ridibunda* from the Caspian Sea region (type-locality) were recorded and studied (SCHNEIDER & EGIASARJAN, 1991) and compared with those from various East European and West Asian regions (SCHNEIDER & SINSCH, 1992), and no significant differences were found. However, no such comparisons were made involving mating calls recorded in Central, Northern and Western Europe. Obvious differences in general aspect, colours and size, between frogs from the latter areas and those from East Europe and Asia point to the possible existence of two distinct species. Future works, using various methods (morphology, protein electrophoresis, caryology, bioacoustics, etc.) will have to address this question. If a distinct species had to be recognized for the European frogs, it should bear the scientific name *Rana (Pelophylax) fortis* (see DUBOIS & OHLER, 1995*a*). The specimens from Poland that we examined in this study are typical for the Central and Western European populations currently referred to *Rana ridibunda*, that include also the Berlin frogs for which the name *Rana fortis* had been proposed.

MATERIAL AND METHODS

ABBREVIATIONS. — MCZ: Museum of Comparative Zoology, Cambridge, Massachusetts, USA; MNHN : Muséum national d'Histoire naturelle, Paris, France; SVL : Snout-vent length.

SPECIMENS STUDIED. — The specimens listed below were measured. Specimens were also studied by electrophoresis, except those whose number is followed below by an asterisk (*). Juveniles, followed below by the sign #, were used only for the computation of values shown in Fig. 2, but not of values given in Table II.

Rana perezi Seoane, 1885. — **France**: (A) Pyrénées-Orientales: Banyuls-sur-Mer (42°28'N, 3°07'E): MNHN 1993.3377-3381 (2 adult males and 3 adult females), coll. Jean-Daniel GRAF, March 1976; (B) Bouches-du-Rhône: (1) Faraman (43°25'N, 4°43'E), 2.5 km west of Salin-de-Giraud: MNHN 1991.77, 1991.83, 1991.88 and 1991.94 (adult males), 1991.84#, 1991.87#, 1991.89-93# and 1991.95-96# (5 juvenile males and 4 juvenile females), coll. Alain DUBOIS, 8 September 1977; (2) Fumemorte (43°28'N, 4°42'E), 6 km north of Salin-de-Giraud: MNHN 1991.677 (adult male), 1991.676# and 1991.678# (juvenile male and juvenile female), coll. Alain DUBOIS, 8 September 1977; (3) Saint-Bertrand (43°27'N, 4°39'E), 7 km north-west of Salin-de-Giraud: MNHN 1991.675 (adult female), coll. Alain DUBOIS, 8 September 1977; (4) Collocation (43°26'N, 4°41'E), 3.5 km north-west of Salin-de-Giraud: MNHN 1991.680 (adult male), 1991.679# (juvenile male), coll. Alain DUBOIS, 8 September 1977; (5) Astouin (43°32'N, 4°24'E), 10 km north of Saintes-Maries-de-la-Mer: MNHN 1991.97# (juvenile female), coll. Alain DUBOIS, 5 September 1977; (6) Bac du Petit Sauvage (43°29'N, 4°25'E), 5 km north-west of Saintes-

Maries-de-la-Mer: MNHN 1991.100#, 1991.670# and 1991.672-673# (3 juvenile males and 1 juvenile female), coll. Alain DUBOIS, 5 September 1977. — **Spain**: Galicia: La Coruña: (1) La Coruña (43°22'N, 8°23'W): MCZ 6832* (adult female), coll. D. Victor LOPEZ SEOANE, lectotype of *Rana esculenta perezi*; (2) Cabañas (43°24'N, 8°09'W): MNHN 1889.596* (adult female), coll. D. Victor LOPEZ SEOANE, paralectotype of *Rana esculenta perezi*.

Rana "kl. RP" (GRAF & POLLS PELAZ, 1989). — **France**: (A) Gard: Gorges de l'Aiguillon, between Lussan (44°09'N, 4°22'E) and La Bastide: MNHN 1993.3374-3376 (adult females), coll. Jean-Daniel GRAF, March 1976; (B) Bouches-du-Rhône: (1) Faraman (43°25'N, 4°43'E), 2.5 km west of Salin-de-Giraud: MNHN 1991.76 and 1991.78 (adult females), 1991.79-80 and 1991.82 (subadult females), 1991.85 (juvenile male) and 1991.86 (adult male), coll. Alain DUBOIS, 8 September 1977; (2) Astouin (43°32'N, 4°24'E), 10 km north of Saintes-Maries-de-la-Mer: MNHN 1991.98-99# (juvenile males), coll. Alain DUBOIS, 5 September 1977; (3) Bac du Petit Sauvage (43°29'N, 4°25'E), 5 km north-west of Saintes-Maries-de-la-Mer: 1991.671# and 1991.674# (juvenile males), coll. Alain DUBOIS, 5 September 1977.

Rana ridibunda Pallas, 1771. — **Germany**: Berlin (52°32'N, 13°24'E), lake-like expansion of the river Spree: MNHN 1884.254* (adult female), 1884.255* and 1884.256* (adult males), coll. fisherman NOACK, spring 1884, respectively paralectotype, lectotype and paralectotype of *Rana fortis* Boulenger, 1884. — **Poland**: Poznan Debina: MNHN 1982.2340* (adult female), 1982.2349* (adult male), 1982.2372-2373* (subadult females), 1982.2379* (subadult male), coll. Leszek BERGER, 20 August 1968.

ELECTROPHORESIS. — The specimens of *Rana perezi* and of its associated klepton were identified by electrophoresis, except for old type-specimens. Those from Gard (Gorges de l'Aiguillon) and from Pyrénées-Orientales (Banyuls-sur-Mer) were part of those studied and reported upon by GRAF *et al.* (1977), for which the following enzyme loci were studied: LDH-B, CK, AAT-1 and AAT-2. Those from Bouches-du-Rhône (Camargue) were identified on the basis of LDH alone, which is clearly diagnostic for the distinction of the two taxa; the method used for this electrophoresis is described in TUNNER (1980: 261-262).

MEASUREMENTS. — Twenty-six measurements (Table I) were taken from all specimens with caliper or binocular microscope. Except for *Rana ridibunda*, only electrophoretically determined adults and subadults were included in the morphometrical analysis which led to values given in Table II. Since the aim of this work was to find diagnostic measurements, we discarded in the results those measurements and ratios which did not show significant differences between the three frog taxa studied.

STATISTICS. — Despite the low numbers of specimens studied, these numbers are enough for a statistical analysis using non-parametric tests with a level of significance of .001 (see *e.g.* DUBOIS, 1984). Mean, standard deviation and range were computed for all variables of all groups on a personal computer with SPSS program (NORUSIS, 1992). The standard non-parametric Mann-Whitney U test (ZAR, 1984) was used to compare the three groups pairwise.

To compare ratios from adult-subadult and juvenile specimens, we used boxplot sketches (NORUSIS, 1992). These boxplots display summary statistics for the distribution and plot the median, the 25th percentile, the 75th percentile and values more than 1.5 box-lengths from 75th percentile (outliers).

TABLE I. – Description of measurements.
Description des mensurations.

EL	Eye length
EN	Distance from eye to nostril
FLL	Forelimb length (from elbow to base of outer palmar tubercle)
FOTL	Fourth toe length (from base of outer metatarsal tubercle)
HL	Head length (from mandibular articulation to tip of snout)
HW	Head width
IBE	Distance between posterior edges of eyes
IC	Distance between choanae
IFE	Distance between anterior edges of eyes
IMT	Length of inner metatarsal tubercle
IMTH	Height of inner metatarsal tubercle
IN	Internarial space
ITL	Inner toe length (from distal edge of inner metatarsal tubercle)
IV	Distance between proximal edges of vomerine ridges
MBE	Distance from mandibular articulation to posterior edge of eye
MFE	Distance from mandibular articulation to anterior edge of eye
MN	Distance from mandibular articulation to nostril
SVL	Snout-vent length
TFL	Third finger length (from base of proximal subarticular tubercle)
TL	Tibia length
TYD	Greatest tympanum diameter
TYE	Distance from tympanum to back of eye
VRL	Length of vomerine ridge
VTL	Distance between distal edges of vomerine ridges
WOFF	Webbing between fourth and fifth toe (from base of outer metatarsal tubercle)
WOTF	Webbing between third and fourth toe (from base of outer metatarsal tubercle)

NOMENCLATURE OF KLEPTONS. — For the nomenclatural treatment of kleptons, we follow the proposals of DUBOIS & GÜNTHER (1982) and DUBOIS (1991), according to which kleptons are taxa of the species-group that are nomenclaturally of the species rank but that have biological properties different of those of "biological species" ("normal", bisexual species). Kleptons receive scientific Latin names similar to those of species, but which can be distinguished from the latter by the insertion of the sign "kl." between the genus-group name(s) and the species-group name(s). We follow DUBOIS & OHLER (1995*a*) in their placement of European green frogs in the subgenus *Pelophylax* Fitzinger, 1843 of the genus *Rana* Linnaeus, 1758.

DESCRIPTIVE METHODS. — In order to facilitate comparisons, the detailed descriptions of the three type-specimens given below follow the same plan. Webbing formula is presented according to MYERS & DUELLMAN (1982).

RESULTS

MORPHOMETRICAL COMPARISONS OF *RANA PEREZI, RANA RIDIBUNDA* AND GRAF'S FROG

Electrophoretic data obtained from the specimens collected in Bouches-du-Rhône, Gard and Pyrénées-Orientales allowed to refer clearly these specimens to two taxa: *Rana perezi* and its associated hybridogenetic klepton (see GRAF *et al.*, 1977; GRAF & POLLS PELAZ, 1989). For

the research of diagnostic measurements, we pooled all specimens electrophoretically characterized, irrespective of their sexes, ages and localities: thus we had 12 adult and subadult specimens of *Rana perezi* and 9 adult and subadult specimens of Graf's klepton.

Thirty-seven ratios were tested pairwise with the Mann-Whitney U test. Fourteen ratios were found to be diagnostic between *Rana perezi* and Graf's frog (Table II). These measurements are from various parts of the body: head, foot and webbing. Particularly interesting and diagnostic are the measurements which involve the vomerine ridges. The ratios IV/VRL, IV/IC, IV/SVL and also WOTF/FOTL show highly significant differences between our two samples. *Rana perezi* has a greater distance between vomerine ridges (Fig. 1), which appears in the ratios involving IV. It also has a longer foot and a less developed webbing.

The sample of the hybridogenetic klepton is statistically different from *Rana ridibunda* for 16 ratios (Table II). The measurements involve also the different parts of the body. The ratios TYD/IN, TYD/SVL, TYE/SVL and VRL/IC show rather high significant differences between the two samples. *Rana ridibunda*'s tympanum is relatively smaller than in both *Rana perezi* and Graf's frog. The distance between vomerine ridges is somewhat intermediate. *Rana ridibunda* shows the highest development of webbing of the three forms.

Twelve ratios describing the two groups representing *Rana ridibunda* and *Rana perezi* show statistically significant differences (Table II). Seven of these ratios (HW/SVL, IV/IC, IV/VRL, TYD/SVL, TYD/TYE, WOTF/FOTL, WOTF/SVL) show rather high significant differences between the two samples. *Rana perezi* has a clearly narrower head than *Rana ridibunda*, a larger tympanum and tympanum-eye distance, and less webbing on feet. Vomerine ridges and associated features are more separated than in *Rana ridibunda*.

Five ratios show significant differences between all three groups (IV/IC, IV/SVL, IV/VRL, TYD/SVL, TYD/TYE). They concern vomerine ridges' position and tympanum size. Foot measurements of *Rana* kl. RP show intermediate values between *Rana ridibunda* and *Rana perezi*. But the values for vomerine teeth morphology are intermediate in *Rana ridibunda* and extreme in the hybrid.

Some ratios, which are clearly diagnostic between *Rana perezi* and Graf's frog in adults, can also be used cautiously for determination of juveniles of these two forms, as shown here in Fig. 2 for the ratio IV/VRL: out of 42 specimens studied, only one showed an ambiguous value for this ratio.

Of the ratios diagnostic for the complex *Rana lessonae* – *Rana* kl. *esculenta* – *Rana ridibunda* (BERGER, 1973), only one, TL/SVL, shows a significant statistical difference between *Rana ridibunda* and *Rana perezi*.

STUDY OF TWO SYNTYPES OF *RANA ESCULENTA PEREZI* SEOANE, 1885

We were able to study and measure two of the original syntypes of *Rana esculenta perezi* and we computed the ratios shown above to allow morphological distinction of the three taxa studied. Table III shows that the values of most of these ratios fall within the ranges of *perezi*. We conclude that these two syntypes are morphologically similar to the electrophoretically characterized specimens of *Rana perezi*. Designation by DUBOIS & OHLER (1995*a*) of one of these two syntypes as lectotype of *perezi* was therefore appropriate to stabilize definitely the nomenclatural status of this name. A detailed description of this lectotype is provided below.

DESCRIPTIONS OF TYPE-SPECIMENS

Rana (Pelophylax) kl. **grafi** kl. nov.
(Figs 1a, 3)

HOLOTYPE. — MNHN 1993.3374, adult female (SVL 111.0 mm), collected by Jean-Daniel GRAF in the Gorges de l'Aiguillon, between Lussan (44°09'N, 4°22'E) and La Bastide, Gard, France, in March 1976.

PARATYPES. — MNHN 1993.3375-3376, adult females (SVL 94.5 mm and 56.9 mm), same collection data as the holotype. MNHN 1991.76, adult female (SVL 71.9 mm), 1991.78, adult female (SVL 66.5 mm), 1991.79-80, subadult females (SVL 91.0 and 71.2 mm), 1991.82, subadult female (SVL 55.2 mm), 1991.85, juvenile male (SVL 39.2 mm) and 1991.86, adult male (SVL 33.9 mm), collected by Alain DUBOIS at Faraman (43°25'N, 4°43'E), 2.5 km west of Salin-de-Giraud, Bouches-du-Rhône, France, on 8 September 1977. MNHN 1991.98-99, juvenile males (SVL 27.6 mm and 36.5 mm), collected by Alain DUBOIS at Astouin (43°32'N, 4°24'E), 10 km north of Saintes-Maries-de-la-Mer, Bouches-du-Rhône, France, on 5 September 1977. MNHN 1991.671 and 1991.674, juvenile males (SVL 29.9 mm and 24.9 mm), collected by Alain DUBOIS near the Bac du Petit Sauvage (43°29'N, 4°25'E), 5 km north-west of Saintes-Maries-de-la-Mer, Bouches-du-Rhône, France, on 5 September 1977.

NOTE ON PARATYPES. — Paratypes are morphologically similar to the holotype.

ETYMOLOGY OF SPECIES-GROUP NAME. — We dedicate this frog to Jean-Daniel GRAF who discovered this new klepton and kindly provided us with some of the specimens he had studied by electrophoresis.

DIAGNOSIS

A large-sized green frog. It can be distinguished morphologically from *Rana perezi* by more webbing on feet and higher metatarsal tubercle. It differs from *Rana ridibunda* by its smaller head width, eye-tympanum distance smaller than half of tympanum diameter, shorter fourth toe and lesser webbing. Of both taxa, Graf's frog is distinguished by its smaller intervomer distance, longer vomerine teeth ridges and smaller ratio of vomerine ridge length by intervomer distance. Electrophoretic characteristics of this taxon were published by GRAF *et al.* (1977).

DESCRIPTION OF HOLOTYPE

Specimen with tissue sampling, snout-vent length 111.0 mm. Head slightly longer (35.2 mm) than broad (34.0 mm); snout moderately pointed, slightly protruding beyond mouth, slightly shorter (8.2 mm) than diameter of eye (8.6 mm); canthus rostralis rounded, loreal region abrupt, concave; interorbital space flat, smaller (4.3 mm) than both internarial distance (5.1 mm) and upper eyelid width (6.8 mm); nostril slightly nearer (7.4 mm) to eye than to tip of snout (8.2 mm); tympanum present, its diameter (6.9 mm) more than two third of diameter of eye, its distance to eye (5.1 mm) roughly three fourth of its diameter; vestige of pineal eye absent; tongue ovally elongated, emarginated behind, finely granulated. Vomerine teeth between choanae in two ridges forming an angle of 150°; ridges long (6.3 mm), 63.0 times the separation between them (0.1 mm).

Arm short, forearm (19.8 mm) shorter than hand (23.5 mm); finger length, shortest to longest: II < I < IV < III; length of third finger 13.8 mm; tips of fingers pointed; three metacarpal tubercles, moderately developed; supernumerary tubercle on base of finger III; subarticular tubercles rounded, moderately developed.

Hind limbs moderately long, shank three times longer (48.2 mm) than broad (15.1 mm), slightly shorter than thigh (50.9 mm); shank and thigh both shorter than distance from base of inner metatarsal tubercle to tip of toe IV (51.6 mm); toes moderately long, length of IV (30.6 mm)

TABLE II. — Results of Mann-Whitney U-test comparing some morphometric ratios of adults and subadults of *Rana perezi* (P; n = 13), *Rana* kl. *grafi* (G; n = 8) and *Rana ridibunda* (R; n = 5). Ranges, mean and standard deviation are given for each species. Significance level : *** 0.001; ** 0.010; * 0.050.

Résultats de la comparaison par le test U de Mann-Whitney de quelques rapports morphométriques chez des adultes et subadultes de Rana perezi *(P ; n = 13),* Rana *kl.* grafi *(G ; n = 8) et* Rana ridibunda *(R ; n = 5). Pour chaque espèce sont données les valeurs extrêmes du rapport, la moyenne et l'écart-type. Coefficients de risque : *** 0.001 ; ** 0.010 ; * 0.050.*

Ratio	*Rana perezi*	*Rana* kl. *grafi*	*Rana ridibunda*	P × R	P × G	R × G
FOTL/SVL	0.560 ± 0.053 0.479 – 0.632	0.536 ± 0.042 0.455 – 0.588	0.582 ± 0.015 0.556 – 0.595			*
HW/SVL	0.341 ± 0.012 0.322 – 0.359	0.351 ± 0.024 0.306 – 0.393	0.376 ± 0.015 0.353 – 0.393	**		*
IBE/SVL	0.236 ± 0.021 0.192 – 0.268	0.314 ± 0.017 0.179 – 0.230	0.221 ± 0.017 0.204 – 0.239		*	
IC/SVL	0.099 ± 0.010 0.082 – 0.115	0.086 ± 0.007 0.071 – 0.097	0.096 ± 0.005 0.091 – 0.102		*	*
IMT/SVL	0.051 ± 0.006 0.038 – 0.059	0.054 ± 0.006 0.048 – 0.065	0.047 ± 0.006 0.044 – 0.057			*
IN/SVL	0.069 ± 0.009 0.053 – 0.084	0.058 ± 0.007 0.046 – 0.069	0.062 ± 0.006 0.056 – 0.069		**	
IV/IC	0.11 ± 0.03 0.066 – 0.171	0.03 ± 0.02 0.013 – 0.060	0.06 ± 0.01 0.046 – 0.073	**	***	*
IV/SVL	0.011 ± 0.004 0.006 – 0.018	0.003 ± 0.002 0.001 – 0.005	0.006 ± 0.001 0.004 – 0.007	*	***	*
IV/VRL	0.346 ± 0.139 0.192 – 0.692	0.008 ± 0.004 0.003 – 0.016	0.158 ± 0.032 0.123 – 0.200	**	***	*
THL/SVL	0.494 ± 0.029 0.448 – 0.559	0.517 ± 0.022 0.467 – 0.534	0.781 ± 0.023 0.457 – 0.509		*	*
TL/SVL	0.507 ± 0.034 0.445 – 0.557	0.531 ± 0.037 0.459 – 0.574	0.551 ± 0.018 0.525 – 0.566	*		
TYD/IN	1.34 ± 0.30 1.00 – 2.00	1.86 ± 0.19 1.61 – 2.22	1.11 ± 0.10 0.973 – 1.19		**	**
TYD/SVL	0.091 ± 0.008 0.081 – 0.108	0.106 ± 0.005 0.099 – 0.111	0.069 ± 0.003 0.066 – 0.072	**	**	**
TYD/TYE	2.86 ± 0.71 1.79 – 4.25	2.16 ± 0.21 1.83 – 2.39	1.88 ± 0.22 1.68 – 2.25	**	*	*
TYE/SVL	0.034 ± 0.011 0.021 – 0.049	0.050 ± 0.006 0.044 – 0.059	0.037 ± 0.005 0.029 – 0.042		*	**
VRL/IC	0.34 ± 0.07 0.246 – 0.480	0.43 ± 0.04 0.365 – 0.482	0.36 ± 0.02 0.336 – 0.373		**	**
VRL/SVL	0.047 ± 0.018 0.026 – 0.073	0.080 ± 0.023 0.057 – 0.132	0.069 ± 0.007 0.059 – 0.074	*	**	
WOFF/SVL	0.339 ± 0.034 0.291 – 0.400	0.364 ± 0.034 0.312 – 0.405	0.384 ± 0.012 0.368 – 0.402	*		*
WOTF/FOTL	0.59 ± 0.06 0.435 – 0.648	0.67 ± 0.03 0.617 – 0.715	0.68 ± 0.02 0.638 – 0.697	**	***	
WOTF/SVL	0.330 ± 0.035 0.284 – 0.397	0.358 ± 0.026 0.312 – 0.386	0.394 ± 0.010 0.380 – 0.405	**		*
WOTF/WOFF	0.976 ± 0.046 0.899 – 1.05	0.987 ± 0.033 0.945 – 1.06	1.03 ± 0.020 1.01 – 1.06	*		*

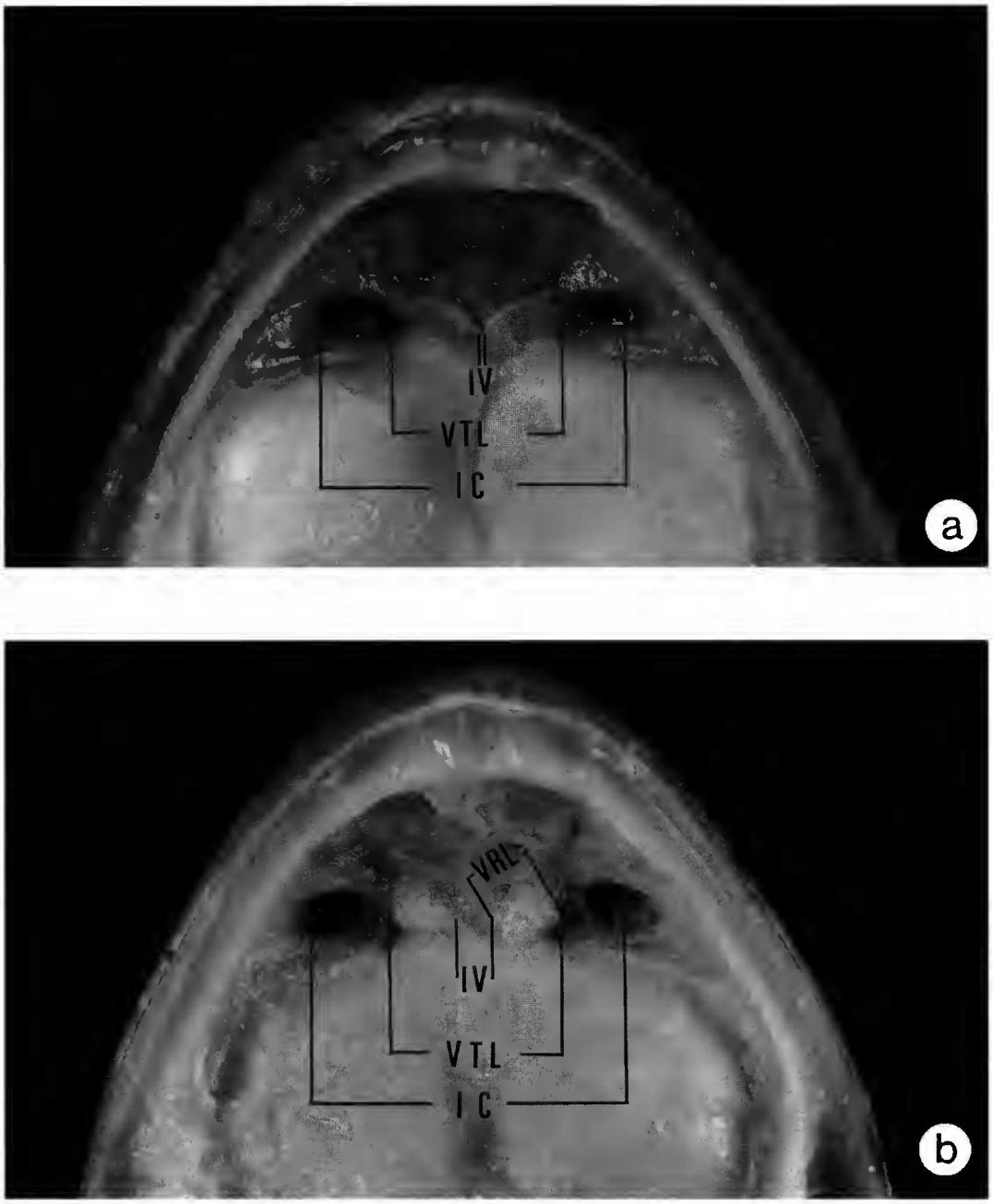

FIG. 1. — Vomerine teeth position in (a) *Rana* kl. *grafi* (MNHN 1993.3374, holotype) and (b) *Rana perezi* (MNHN 1993.3377). Scale: 5 mm. For the meaning of abbreviations, see Table I.

Position des dents vomériennes chez (a) Rana *kl.* grafi *(MNHN 1993.3374, holotype) et (b)* Rana perezi *(MNHN 1993.3377). Échelle : 5 mm. Pour la signification des abréviations, voir le tableau I.*

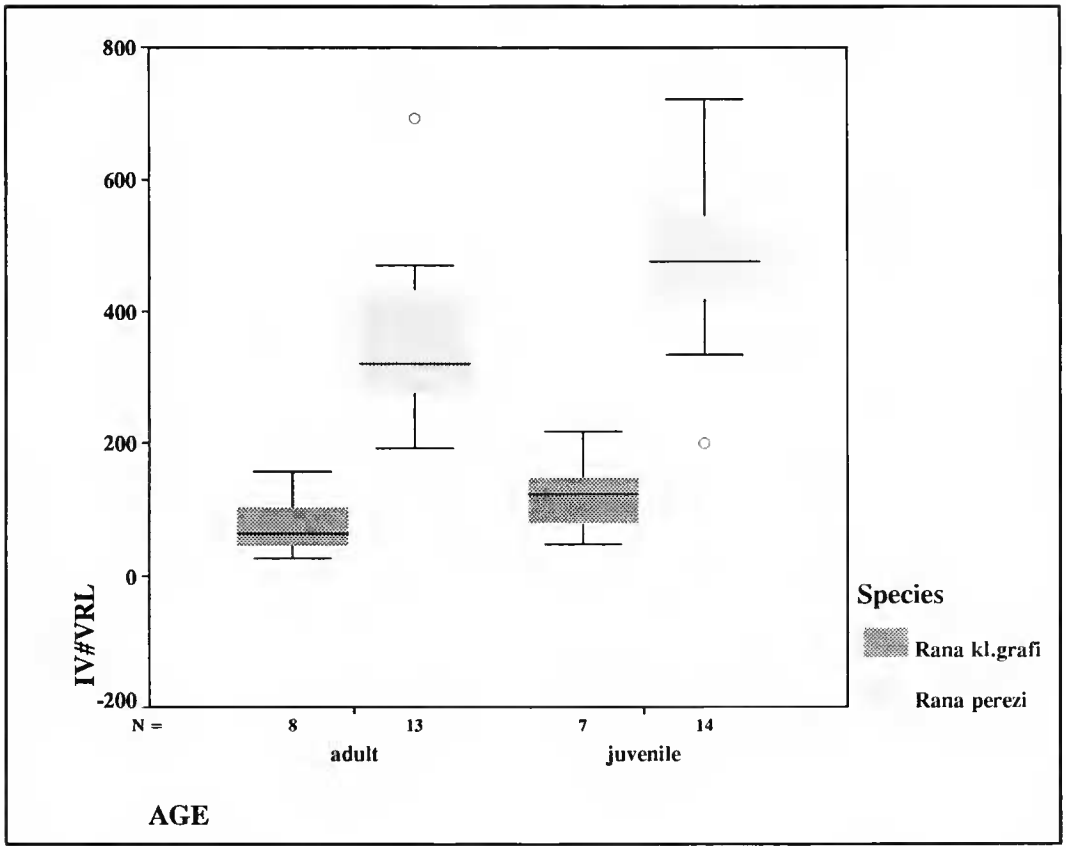

FIG. 2. — Boxplot sketches displaying summary statistics for the ratio IV/VRL in adult-subadult and juvenile specimens of *Rana* kl. *grafi* and *Rana perezi*. The median, the 25th percentile, the 75th percentile and outliers are plotted. N: number. For the meaning of other abbreviations, see Table I.

Diagramme « boxplot » montrant les paramètres statistiques principaux pour le rapport IV/VRL chez des spécimens adultes-subadultes et juvéniles de Rana *kl.* grafi *et* Rana perezi. *La médiane, le 25e percentile, le 75e percentile et les valeurs excentriques (« outliers ») sont figurés. N: nombre. Pour la signification des autres abréviations, voir le tableau I.*

less than one half of length from base of tarsus to tip of toe IV (72.6 mm); tips of toes rounded; webbing moderately developed (I 1/2 – 1 II 1/2 – 1 1/2 III 1/2 – 1 1/2 IV 1 – 1/2 V); inner metatarsal tubercle moderately developed, its length (5.3 mm) 2.9 times in length of toe I (15.5 mm); glandular ridge on tarsus prominent.

Dorsum with large flat warts, also between eyes; two broad glandular dorsolateral ridges; ventral surfaces smooth.

Colour in alcohol: Brownish with few large darker spots; a slightly clearer mediodorsal line; dorsolateral folds darker brown; forelimbs without darker spots; hind limbs with few darker bands; ventral surface cream and brown marbled, blurred; back of thigh dark brown with brown spots.

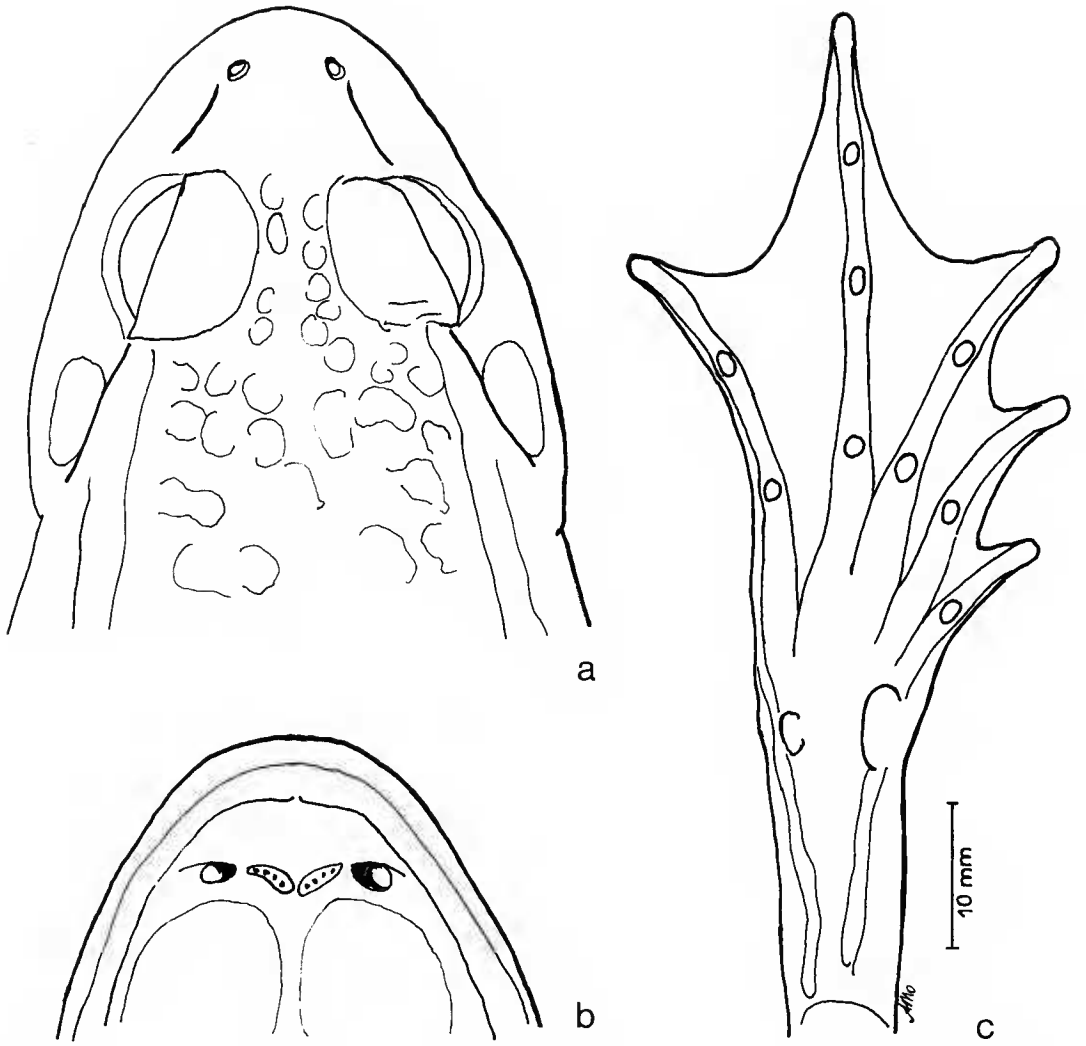

FIG. 3. — *Rana (Pelophylax)* kl. *grafi* kl. nov., MNHN 1993.3374 (holotype): (a) dorsal view of head; (b) roof of mouth; (c) ventral view of right foot.

Rana (Pelophylax) *kl.* grafi *kl. nov., MNHN 1993.3374 (holotype): (a) vue dorsale de la tête; (b) plafond buccal; (c) vue ventrale du pied droit.*

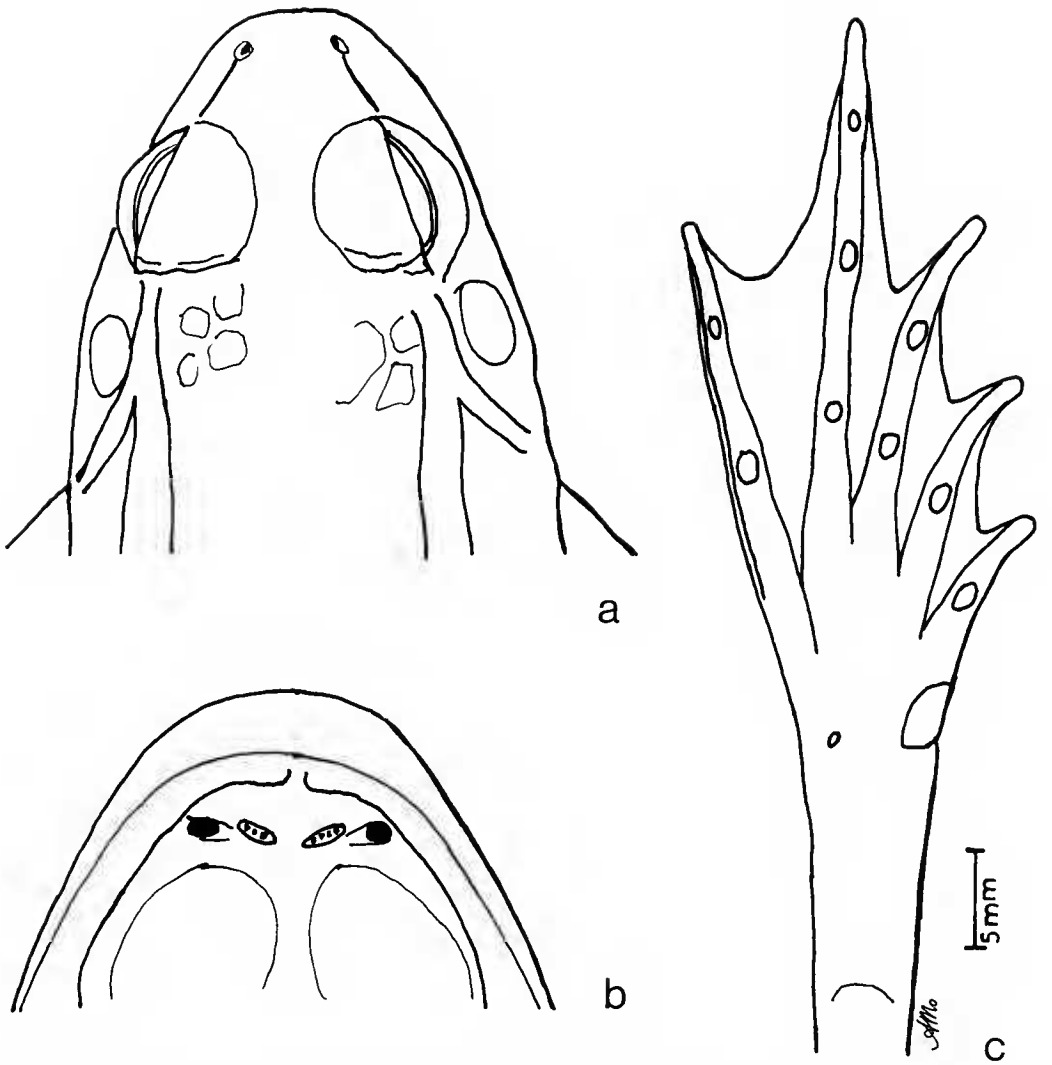

FIG. 4. — *Rana (Pelophylax) perezi* Seoane, 1885, MCZ 6832 (lectotype): (a) dorsal view of head; (b) roof of mouth; (c) ventral view of right foot.

Rana (Pelophylax) perezi *Seoane, 1885, MCZ 6832 (lectotype): (a) vue dorsale de la tête; (b) plafond buccal; (c) vue ventrale du pied droit.*

Rana (Pelophylax) perezi Seoane, 1885
(Figs 1b, 4)

LECTOTYPE (BY DESIGNATION OF DUBOIS & OHLER, 1995a) OF *RANA ESCULENTA PEREZI* SEOANE, 1885: 171. — MCZ 6832, adult female (SVL 63.6 mm), collected by D. Victor LOPEZ SEOANE near La Coruña (43°22'N, 8°23'W), Galicia, Spain, from Fernand LATASTE's collection.

PARALECTOTYPE OF *RANA ESCULENTA PEREZI* SEOANE, 1885: 171. — MNHN 1889.596, adult female (SVL 71.5 mm), from Cabañas (43°24'N, 8°09'W), Galicia, Spain, donation of Victor LOPEZ SEOANE to the Paris Museum on 9 November 1889.

NOTE ON PARALECTOTYPE. — The paralectotype studied is similar to the lectotype, except that it shows an asymmetry in its vomerine teeth. Other paralectotypes may possibly be found in the future, in other Museums where SEOANE or LATASTE may have deposited some of the original syntypes of this taxon.

DIAGNOSIS

A medium-sized green frog. It can be distinguished morphologically from *Rana* kl. *grafi* by less webbing on its feet and its smoother metatarsal tubercle. It differs from *Rana ridibunda* by its smaller head, tympanum closer to eye, shorter hand and foot. It has a larger intervomer distance than both *Rana ridibunda* and *Rana* kl. *grafi*.

DESCRIPTION OF LECTOTYPE

Well-preserved specimen, snout-vent length 63.6 mm. Head slightly longer (22.9 mm) than broad (21.8 mm); snout rounded, not protruding beyond mouth, longer (10.4 mm) than diameter of eye (7.7 mm); canthus rostralis rounded, loreal region abrupt, concave; interorbital space flat, smaller (1.9 mm) than both internarial distance (4.2 mm) and upper eyelid width (4.6 mm); nostril slightly nearer (4.8 mm) to eye than to tip of snout (5.3 mm); tympanum present, its diameter (4.1 mm) more than half of diameter of eye, its distance to eye (1.4 mm) roughly one third of its diameter; vestige of pineal eye absent, tongue ovally elongated, deeply emarginated behind, finely granulated. Vomerine teeth between choanae in two ridges forming an angle of 140°; ridges long (1.94 mm), 3.1 times the separation between them (0.62 mm).

Arm short, forearm (11.2 mm) shorter than hand (14.2 mm); finger length, shortest to longest: I < II < IV < III; length of third finger 8.5 mm; tips of fingers pointed; metacarpal tubercles not distinct, subarticular tubercles rounded, moderately developed.

Hind limbs relatively short, shank almost three times longer (28.3 mm) than broad (11.3 mm), slightly shorter than thigh (29.1 mm); shank and thigh both shorter than distance from base of inner metatarsal tubercle to tip of toe IV (34.6 mm); toes moderately long, length of IV (19.2 mm) less than one third of length from base of tarsus to tip of toe IV (46.9 mm); tips of toes pointed; webbing moderately developed (I 1/2 – 2 II 1 – 2 III 1 – 2 IV 2 – 1 V); inner metatarsal tubercle moderately developed, its length (3.6 mm) 2.3 times in length of toe I (8.3 mm); glandular ridge on tarsus flat.

Dorsum with large flat warts, except on top of head; two broad glandular dorsolateral ridges; ventral surfaces smooth.

Colour in alcohol: Brownish with few large darker spots; a slightly clearer mediodorsal line; dorsolateral folds slightly darker brown; forelimbs with few darker spots; hind limbs with darker spotlike bands; ventral surface cream and brown marbled, very homogeneous; back of thigh blackish with few clearer spots, a dark line separating ventral from dorsal surface.

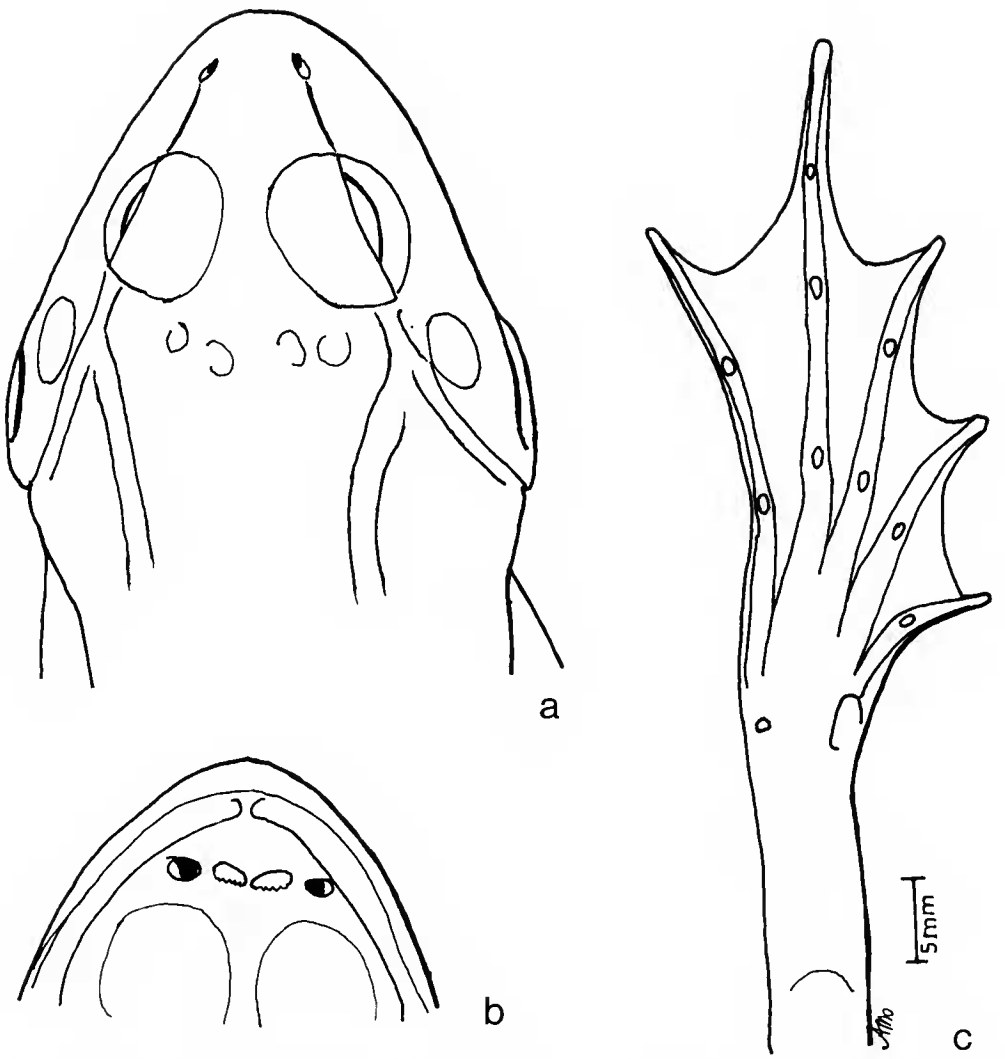

FIG. 5. — *Rana (Pelophylax) ridibunda* Pallas, 1771, MNHN 1884.255 (lectotype of *Rana fortis* Boulenger, 1884): (a) dorsal view of head; (b) roof of mouth; (c) ventral view of right foot.

Rana (Pelophylax) ridibunda *Pallas, 1771, MNHN 1884.255 (lectocype de* Rana fortis *Boulenger, 1884): (a) vue dorsale de la tête; (b) plafond buccal; (c) vue ventrale du pied droit.*

Rana (Pelophylax) ridibunda Pallas, 1771
(Fig. 5)

LECTOTYPE (BY DESIGNATION OF DUBOIS & OHLER, 1995*a*) OF *RANA FORTIS* BOULENGER, 1884: 220. — MNHN 1884.255, adult male (SVL 71.4 mm), collected by fisherman NOACK in a lake-like expansion of the river Spree, near Berlin, Berlin, Germany.

PARALECTOTYPES OF *RANA FORTIS* BOULENGER, 1884: 220. — MNHN 1884.254, adult female (SVL 70.5 mm) and 1884.256, adult male (SVL 70.5 mm), same collection data as the lectotype.

NOTE ON PARALECTOTYPES. — Both paralectotypes studied are similar in size and colour to the lectotype. Other paralectotypes will certainly be found in the future in other Museums, as BOULENGER (1884) described this species using a series of 85 syntypes.

DIAGNOSIS

A large-sized green frog. Webbing of foot more important than in *Rana perezi* and *Rana* kl. *grafi*. Head larger than in these two taxons, tympanum-eye distance larger than half of tympanum diameter, vomerine teeth position intermediate.

DESCRIPTION OF LECTOTYPE OF *RANA FORTIS* BOULENGER, 1884

Slightly dried alcohol fixed specimen, snout-vent length 71.4 mm. Head longer (28.3 mm) than broad (26.0 mm); snout rounded, not protruding beyond mouth, longer (10.4 mm) than diameter of eye (7.6 mm); canthus rostralis rounded, loreal region abrupt, concave; interorbital space flat, smaller (2.3 mm) than both internarial distance (4.0 mm) and upper eyelid width (4.9 mm); nostril slightly nearer (5.5 mm) to eye than to tip of snout (5.3 mm); tympanum present, its diameter (5.3 mm) more than half of diameter of eye, its distance to eye (2.9 mm) roughly one half of its diameter; vestige of pineal eye absent, tongue ovally elongated, deeply emarginated behind, finely granulated. Vomerine teeth between choanae in two ridges forming an angle of 130°; ridges long (1.59 mm), 4.9 times the separation between them (0.34 mm).

Arm short, forearm (16.3 mm) shorter than hand (18.4 mm); finger length, shortest to longest: I = II < IV < III; length of third finger 9.9 mm; tips of fingers pointed; metacarpal tubercles not distinct, subarticular tubercles rounded, moderately developed.

Hind limbs relatively short, shank four times longer (36.1 mm) than broad (8.3 mm), longer than thigh (29.6 mm); shank and thigh both shorter than distance from base of inner metatarsal tubercle to tip of toe IV (41.2 mm); toes moderately long, length of IV (24.0 mm) more than one third of length from base of tarsus to tip of toe IV (56.2 mm); tips of toes pointed; webbing moderately developed (I 1/2 – 1 1/2 II 1/2 – 2 III 1 – 2 IV 2 – 1/2 V); inner metatarsal tubercle moderately developed, its length (3.4 mm) 3.4 times in length of toe I (11.6 mm); glandular ridge on tarsus flat.

Dorsum with large flat warts, except on top of head; two broad glandular dorsolateral ridges; ventral surfaces smooth.

Colour in alcohol: Grayish with few large darker spots; a slightly clearer mediodorsal line; dorsolateral folds slightly clearer; forelimbs with few darker spots; hind limbs with darker bands; ventral surface whitish marbled with black, very homogeneous; back of thigh blackish with few clearer spots. Vocal sacs blackish, nuptial pads on finger I blackish.

TABLE III. — Some morphometric ratios of type-specimens, allowing comparison with electrophoretically studied material. Values followed by an asterisk * fall outside the range of variation for the taxon given in Table II. (–): measurement not possible due to injuries. H: holotype; L: lectotype; PL: paralectotype.

Quelques rapports morphométriques chez quelques spécimens-types, permettant une comparaison avec les spécimens étudiés par électrophorèse. Les valeurs suivies d'un astérisque tombent en dehors de l'intervalle de variation donné pour le taxon dans le tableau II. (–): mensuration impossible en raison de blessures. H: holotype; L: lectotype; PL: paralectotype.

	Rana perezi		*Rana* kl. *grafi*	*Rana fortis*		
Ratio	MCZ 6832 L (adult ♀)	MNHN 1889.596 PL (adult ♀)	MNHN 1993.3374 H (adult ♀)	MNHN 1884.255 L (adult ♂)	MNHN 1884.254 PL (adult ♀)	MNHN 1884.256 PL (adult ♂)
FOTL / SVL	0.511	0.502	0.481	0.577	0.580	–
HW / SVL	0.343	0.351	0.332	0.364	0.363	0.369
IBE / SVL	0.218	0.234	0.179	0.200	0.217	0.203
IC / SVL	0.0933*	0.0909*	0.0712	0.0862*	0.101	0.0938
IMT / SVL	0.0591	0.0643	0.0478	0.0476	0.0511	0.0440
IN / SVL	0.0622*	0.0573	0.0460	0.0672	0.0644	0.0634
IV / IC	0.0997	0.0923	0.0127	0.0612	0.0436*	0.0470
IV / SVL	0.0093	0.0084	0.00097	0.0052	0.0044	0.044
IV / VRL	0.073	0.231	0.0282	0.183	0.127	0.172
THL / SVL	0.446	0.464	0.467	0.458	0.507	0.507
TL / SVL	0.459	0.464	0.459	0.505*	0.504*	0.509*
TYD / IN	1.225*	1.342*	1.373	1.104	1.171	1.073
TYD / SVL	0.0762*	0.0769*	0.0681	0.0754	0.0754*	0.0680
TYD / TYE	2.882*	2.75*	1.353	1.822	1.907	1.762
TYE / SVL	0.0264*	0.0280*	0.0331	0.0409	0.0395	0.0386
VRL / IC	0.367	0.379	0.482	0.296*	0.345	0.273*
VRL / SVL	0.0342	0.0344	0.0568	0.0253*	0.0349	0.0256*
WOFF / SVL	0.311	0.305	0.331	0.377	0.392	0.369
WOTF / FOTL	0.598	0.618	0.674	0.695	0.691	0.667
WOTF / SVL	0.306	0.311	0.324	0.389	0.401	0.380
WOTF / WOFF	0.984	1.020	0.979	1.032	1.018	1.030

DISCUSSION

Morphological distinction between *Rana perezi* and *Rana* kl. *grafi*

In our view, one of the goals of contemporaneous systematists should be to reconcile modern and traditional methods of biology to ensure continuity in science. Studies of genotypes allow understanding of genetic mechanisms involved in the evolution of taxa. But such methods cannot be used without heavy investigations and should be paired with study of external characters and morphology. On the basis of studies linking morphological and genetic information, keys based on purely morphometrical characters can be worked out. Such keys are necessary for work on collection material, field work, and preparation of distribution maps. Until now, most information collected in the past by ancient authors on the distribution of green frogs is obsolete, as the level of determination depended on the worker. To prepare well-founded keys would permit to go further in our knowledge about biogeography and evolution of green frogs.

The morphologies of *Rana perezi* and *Rana* kl. *grafi* had not been compared until now. This paper is a first step in this respect. Even if the sample is small, clear (significant) morphometrical differences were found between two electrophoretically determined groups of frogs. These characters permit identification of frogs for which no electrophoretic data are available.

The morphometric ratios traditionally used for species identification in the complex *lessonae – esculenta – ridibunda* do not work in the complex *perezi – grafi – ridibunda*. In the latter complex, the differentiation is more important in foot and vomerine teeth morphologies than in tibia, inner metatarsal tubercle, and inner toe lengths. This shows clearly that morphological studies should not only include characters that were valid for certain groups of species ("good" characters), but that the analysis should embrace the whole morphology, including measurements that concern all parts of the body.

Because of the small number of electrophoretically determined specimens available, in this study we pooled specimens from different populations, of the two sexes and of various ages and sizes. We excluded young specimens, because usually in frogs morphological changes are very important during ontogeny, mostly as a result of allometric growth. In the future, it will be interesting to investigate about variation between different populations and to include more taxa for comparison. But, to correctly study such a problem, close attention should be paid to the important intrapopulational variations in frogs due to sexual dimorphism and allometric growth.

In some of the studied ratios, *Rana* kl. *grafi* is intermediate between the two non-hybrid species. This might be a consequence of the hybrid origin of the klepton. In other ratios, *Rana* kl. *grafi* shows distinct new characters. Vomerine teeth position is not like in any of the two non-hybrid species, nor is it intermediate. It is clearly a new character.

Nomenclatural problems

A major aim of this study was to solve nomenclatural problems concerning green frogs from Southern France and Iberian Peninsula using the most parsimonious way. In a first step we defined morphometrical differences between the two taxa occurring there. Then we used these characters for phenotypical determination of the lectotype and one paralectotype of *Rana*

esculenta perezi Seoane, 1885: this study confirmed that both specimens are members of the non-hybrid taxon. This determination is consistent with the fact that only non-hybrid specimens have been found in Western Spain until now (UZZELL & TUNNER, 1983; ARANO *et al.*, 1995). This solves the first nomenclatural problem. The second is solved by the proposal in this paper of a new scientific name, *Rana* kl. *grafi*, for the klepton found associated with *Rana perezi* in some areas.

HISTORICAL CONSIDERATIONS

European green frogs seem to be a monophyletic group closely related to East Asian green frogs (UZZELL, 1982), with which they constitute the subgenus *Pelophylax* (DUBOIS, 1992). Within the Western green frogs, *Rana perezi* and *Rana saharica* seem to form a monophyletic group (UZZELL, 1982; BEERLI, 1993). This group probably was isolated on the African continent when the Mediterranean Sea was formed. Immigration to the Iberian Peninsula was made possible by the closing of the Straits of Gibraltar. Estimated divergence time between *Rana perezi* and *Rana saharica* corresponds to the date of reopening of the Straits of Gibraltar (BEERLI, 1993).

Currently, the Northern half of France is occupied by the L-E system (UZZELL & BERGER, 1975), *i.e.* mixed populations of *Rana lessonae* and *Rana* kl. *esculenta*, while the southern part of the country is occupied by the P-RP system (GRAF & POLLS PELAZ, 1989) or P-G system, *i.e.* mixed populations of *Rana perezi* and *Rana* kl. *grafi*. Besides, there is evidence of occurrence of isolated populations of *Rana ridibunda* in various parts in France (CASTANET & GUYÉTANT, 1989; CROCHET, DUBOIS & OHLER, unpubl.). The origin of the latter frogs is unknown: some populations (near universities, etc.) are probably introduced (see *e.g.* DUBOIS, 1982), while others are so isolated that such an origin seems unlikely. These frogs have not yet been compared with *Rana ridibunda* of Central and Northern Europe.

Rana perezi seems to have been a rather recent invader of Europe coming from the South. During its expansion it may have come in contact with the more Northern and Eastern European taxa, possibly in Southern France. *Rana* kl. *grafi* would have appeared through hybridization in this contact zone. There may have been primarily direct contact between *Rana perezi* and *Rana ridibunda*, or the *ridibunda* genome may have been transmitted from *esculenta* to *grafi* through hybridization between *perezi* and *esculenta* (DUBOIS & GÜNTHER, 1982: 296).

Other hypotheses can be considered. As the estimated age of European green frogs is much older than the estimated age of immigration of the *perezi-saharica* stock into the Iberian Peninsula, there might have existed a pre-*perezi* frog in South-Western Europe. This might have been the L-E system, progressively replaced by the P-G system, with a contact/hybrid zone that would move northwards with progression of the latter. This would require competitive superiority of the P-G system over the L-E system in this area, which could be experimentally tested. A detailed study of the composition, structure and dynamics of green frog populations in areas where the P-G system probably meets the L-E system (*e.g.* Charente in Western France, Rhône valley, Southern Massif central) might also throw interesting lights on this question. Another hypothesis would be that a *ridibunda*-like species might have been replaced in the Iberian Peninsula by the P-G system. Some of the morphometrical particularities of *grafi* might indicate that the second parental species was somewhat different from the current European *ridibunda*.

Acknowledgements

We warmly thank the following colleagues for the help they provided for this work: Jean-Daniel GRAF (Genève) deposited some of his electrophoretically determined specimens in the Paris Museum collections; Leszek BERGER (Poznan) gave a large collection of Polish frogs to the Paris Museum; Jose P. ROSADO (Harvard, Cambridge) sent us in loan the syntype of *Rana esculenta perezi* kept in the collections of the Museum of Comparative Zoology; Roger BOUR (Paris) provided helpful comments and suggestions; Laurent BESSOL (Paris) kindly prepared the macrophotographs of Fig. 1.

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